

POLEMONIUM ELUSUM (POLEMONIACEAE),
A NEW SPECIES FROM EAST CENTRAL IDAHO, U.S.A.

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ABSTRACT

Botanical inventory of the Salmon-Challis National Forest has led to the discovery of a new species, *Polemonium elusum*. It may be distinguished from congeners by calyx lobes that are green to purplish with whitish, translucent membranes, oblong to spatulate, 0.4–0.7 mm wide connecting them. The presence of the membrane is unique to the genus. It is restricted to nine locations near the Salmon River between Salmon and Challis. In addition to the distinguishing morphometric features, DNA sequence analysis of the ITS1, 5.8s, and ITS2 nuclear ribosomal DNA supports *P. elusum* as a distinct species.

RESUMEN

El inventario botánico del Salmon-Challis National Forest ha permitido el descubrimiento de una nueva especie, *Polemonium elusum*. Puede diferenciarse de sus congéneres por los lóbulos del cáliz que son de verde a púrpúreos conectados por membranas blanquecinas translúcidas de oblongas a espatuladas, 0.4–0.7 mm de anchas. La presencia de la membrana es única en el género. Está restringida a nueve localizaciones cerca del río Salmon entre Salmon y Challis. En adición a las características morfométricas diferenciadoras, el análisis de secuencias de ADN del ITS1, 5.8s, y el ADN nuclear ribosómico ITS2 soportan *P. elusum* como una especie distinta.

INTRODUCTION

This finding follows a sequence of slow but steady botanical discoveries in east central Idaho from the 1980s to the present. Important characters differentiating this species of *Polemonium* from others are calyx lobes that are green to purplish with whitish, translucent membranes, oblong to spatulate, 0.4–0.7 mm wide, connecting them. The presence of the translucent membrane is unique to the genus. Nine localities have been documented. The type locality is at lower Cow Creek where the species is most abundant. Based on both morphological characters and molecular analyses *Polemonium elusum* is distinct.

This species was discovered while conducting a botanical inventory of the Salmon-Challis National Forest during the summer of 2010. This two-year project is one of more than 74 intensive broad-scale floristic inventories conducted by graduate students and staff of the Rocky Mountain Herbarium (Hartman 1992; Hartman et al. 2009; Hartman & Nelson 2011). For examples of published studies see Reif et al. 2009; Kesonie & Hartman 2011, Kuhn et al. 2011.

Polemonium elusum J.J. Irwin & R.L. Hartman, sp. nov. (**Fig. 1**). TYPE: U.S.A. IDAHO. Lemhi Co.: Lemhi Range, lower Cow Creek, 7 air km (4.4 air mi) NE of Ellis, 44.7402°N, 113.9935°W (NAD83), elev. 1440 m, 15 Jun 2011, Hartman, Irwin, & E.E. Stewart 91587 (HOLOTYPE: RM; ISOTYPES: BRY, CIC, COLO, F, GH, ID, IDS, JEPS, MO, MONT, NY, RSA, SFSU, US, WS, WTU).

Polemonium elusum J.J. Irwin & R.L. Hartman; differens a ceteris speciebus e *Polemonium* in calyce lobis connexus a membrana translucens.

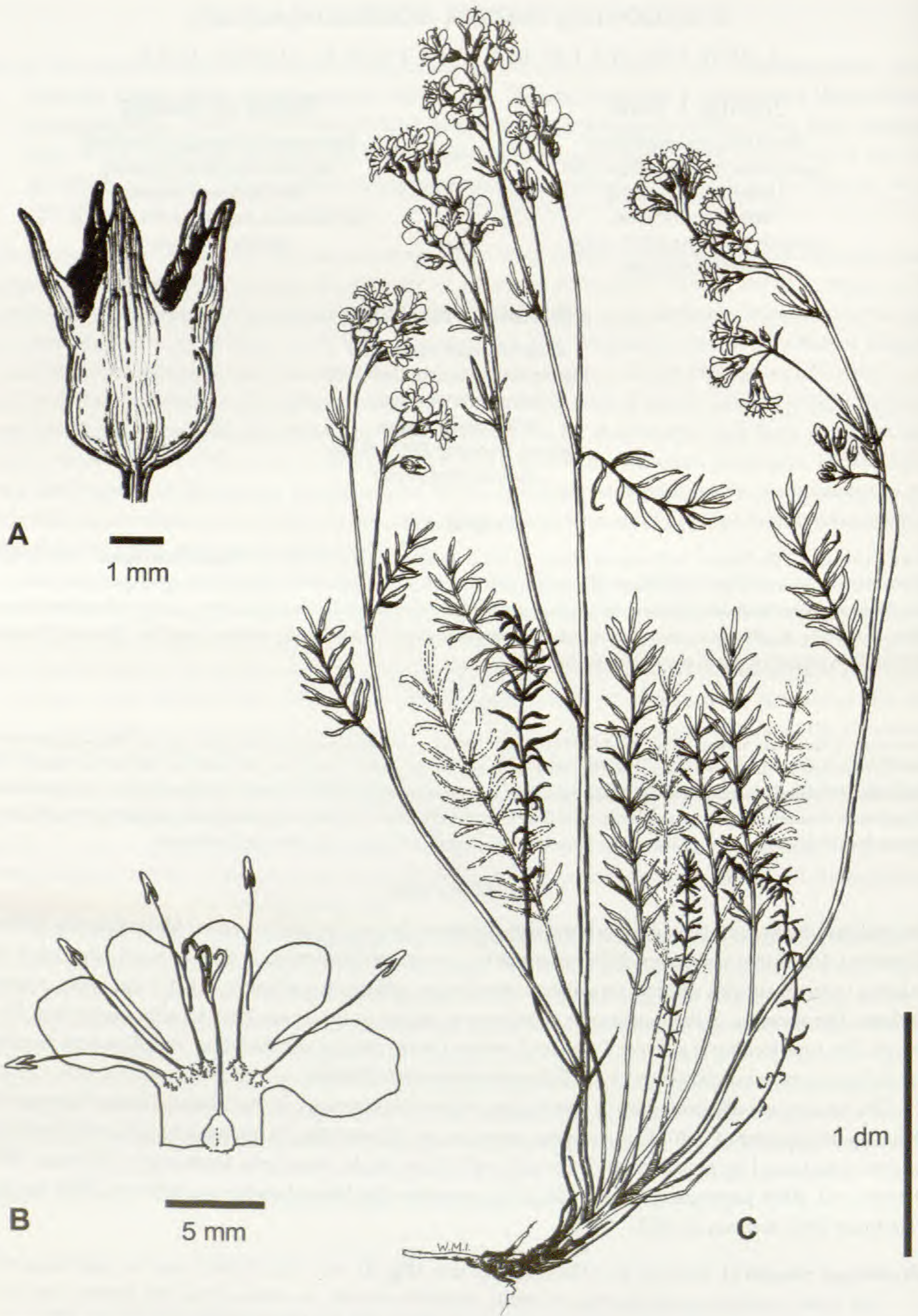


FIG. 1. Illustrations of *Polemonium elusum*, showing: A. calyx, B. longitudinal dissection of a flower, and C. entire plant.

Perennial herbs, caespitose, glabrous to pubescent with trichomes sparse to moderately dense, minute, flaccid to erect, often glandular trichomes, not odiferous; branches subterranean, 3–15. **Stems** 20–50 cm tall. **Leaves** mostly basal and the bases sheathing to scattered along stem, 5–20, 10–30 cm long proximally to 2 cm distally, 1.5–3(–4) wide; petioles 2–7(–11) cm long; pinnae 12–24, mostly 2-parted, alternate or paired and thus appearing whorled, narrowly to broadly elliptic or spatulate, occasionally obovate, 4–28 mm long, 1–3.5 mm wide. **Inflorescences** a thyrses, often diffuse; branches 2–5, 5–11 cm long, strict; flowers 15–60, congested distally; pedicels 5–6 mm long. **Flowers** 5-merous; perianth regular; calyx fused at base, campanulate; lobes lanceolate, green to purplish in part, 4.4–8 mm long, diverging at a 35–40 degree angle; connective membrane in bud, flower, and fruits translucent, whitish, oblong to spatulate, 0.4–0.7 mm wide; sinuses rounded; corolla light blue to white, campanulate, 10–13 mm long, tube 4–5.2 mm long; lobes 5–7.8 mm long, spatulate to obovate; apex rounded, minutely apiculate; stamens usually exerted; filaments attached 2–3 mm above base, at which point minutely and densely tomentose for 0.8–1 mm; anthers basifixed, narrowly to broadly sagittate, broadly elliptic to orbicular following dehiscence, 1.4–1.8 mm long; ovary greenish, broadly ovoid, 2 mm long, with 5 raised nerves at least in part; placentation axile, chambers 3; styles 6.5–8 mm long; branches flattened, 2.5–3.2 mm long; stigma glandular over adaxial surface. **Fruit** globose, tricarpetate, 4.5–5 mm long, split for 60–70 percent of length. **Seeds** brown, trigonous, the abaxial surface rounded, the edges acute, 2.4–2.8 mm long; surface minutely wavy, not mucilaginous.

PARATYPES: U.S.A. IDAHO. Lemhi Co.: Salmon National Forest, Lemhi Range, dry gulch on the north side of Cow Creek, immediately upstream of Black Canyon, 9.5 air km (5.9 air mi) ENE of Ellis, 44.7379°N, 113.9484°W (NAD83), elev. 1,692 m, 17 Jun 2010, *Irwin 1096* (RM); Cow Creek between national forest boundary and the confluence with North Fork Cow Creek, 33.6 air km (20.9 air mi) NE of Challis, 8.8 air km (5.5 air mi) NE of Ellis, 44.7393°N, 113.9605°W (NAD83), elev. 1,600 m, 15 Jun 2011, *Irwin 5038* (RM, SFSU); Salmon River canyon between Salmon and Ellis, slopes above an unnamed wash between Cronks Canyon and Cow Creek, 4.7 air km (2.9 air mi) NE of Ellis, 44.7197°N, 114.006°W (NAD83), elev. 1,493 m, 16 Jun 2011, *Irwin 5148* (RM, SFSU); mountain slopes 0.6 air km S of lower Cow Creek, 6.7 air km NE of Ellis, 44.7308°N, 113.9836°W (NAD83), elev. 1,928 m, 24 Jun 2012, *Irwin 8563* (RM); summit of unnamed mountain east of Cronks Canyon, 6.2 air km ENE of Ellis, 44.7069°N, 113.9738°W (NAD83), elev. 2,560 m, 24 Jun 2012, *Irwin 8570* (RM). **Custer Co.:** Challis National Forest, Pahsimeroi Mountains, upper Gerry Gulch, NW of point 7686, 12.2 air km (7.6 air mi) SW of Ellis, 44.5935°N, 114.1206°W (NAD83), elev. 2,027 m, 24 Jun 2011, *Irwin 5493* (RM); near the creek at upper Gerry Gulch, 11.6 air km (7.2 air mi) SW of Ellis, 44.5976°N, 114.1137°W (NAD83), elev. 2,023 m, 24 Jun 2011, *Irwin 5496* (RM, SFSU); Salmon River Mountains, along Ellis Creek approximately 0.6 air km downstream of Cherry Creek, 5.3 air km WNW of Ellis, 44.6998°N, 114.1141°W (NAD83), elev. 1,582 m, 17 Jun 2012, *Irwin 8452* (RM).

Etymology.—The epithet was chosen as this species has eluded discovery for well over a century, this despite sporadic botanical forays to the region.

Distribution and ecology.—*Polemonium elusum* is known from the mountains and foothills surrounding the town of Ellis, in east central Idaho (Fig. 2). Populations occur from 1440 to 2560 m in elevation, where vegetation transitions from sagebrush and mountain mahogany to Douglas-fir woodland, depending on slope and aspect. Within this range of vegetation, it was found in a variety of microhabitats, thus the species appears to be an ecological generalist. Microhabitats in which plants are found include the margins of talus fields, dry Douglas-fir woodland, outer riparian margins, and shaded rock outcrops. Plants occur in stable but loose, coarse textured colluvial soils. All populations were found on various geologic units of the Challis volcanics group (Zientek et al. 2005) and were most abundant from lower Cow Creek southward across the adjacent unnamed mountain.

The initial discovery was made by Irwin on Cow Creek in mid-June 2010. This locality was surveyed as potential habitat for *Cryptantha salmonensis* Payson, *Astragalus amblytropis* Barneby, and *Oxytropis besseyi* (Rydb.) Blank. var. *salmonensis* Payson. None of these endemics was encountered, but *Polemonium elusum* was found growing under more mesic conditions than would be expected for the aforementioned taxa. Further inventory has shown that populations of *P. pulcherrimum* var. *pulcherrimum* surround the distribution of *P. elusum*. These species have several similarities, including overlapping elevation ranges, dry habitats, and a similar architecture of the corolla and the inflorescence. Additionally, *P. viscosum* has been observed as low as 1770 m elev. in deep canyons above the Salmon River to the north and south of *P. elusum*. However, these congeners have not been found growing sympatrically.

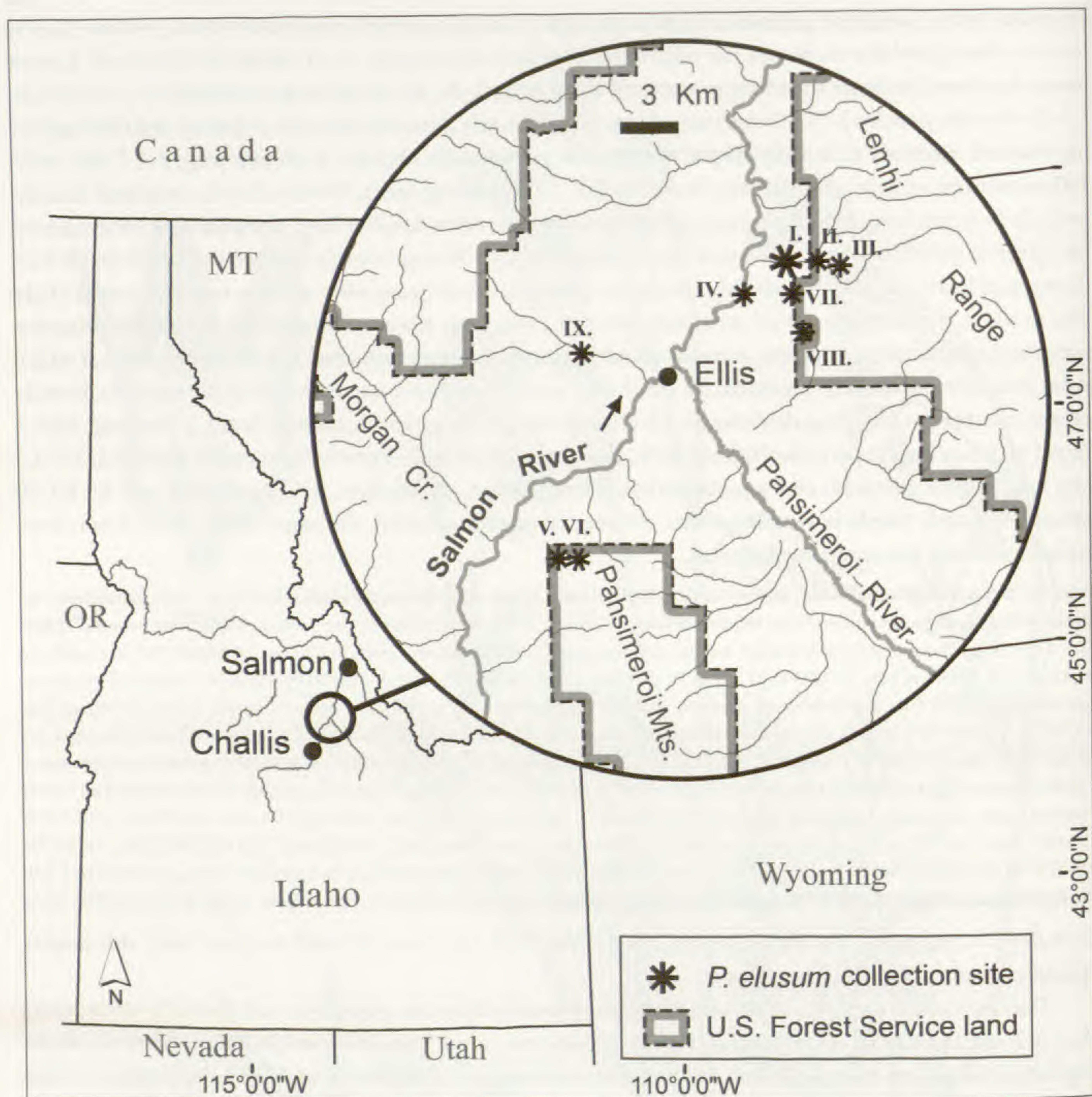


FIG. 2. Distribution of *Polemonium elusum*. Sites are as follows: I. type locality on lower Cow Creek, and collections from II. middle Cow Creek, III. dry gulch off Cow Creek upstream of Black Canyon, IV. unnamed gulch near Cronks Canyon, V. upper Gerry Gulch, VI. upper Gerry Gulch near creek, VII. slopes south of Cow Creek, VIII. unnamed summit ridge south of Cow Creek, and IX. Ellis Creek.

Phenology.—Flowering begins in late-May at more xeric, low elevation sites, continuing through mid-July at higher, cooler sites; fruiting from mid-June through August.

Conservation.—Perhaps the greatest threat to the existence of *Polemonium elusum* is the small total population size and its narrow distribution. The known populations total about 1,300 plants, occupying eight km². Other probable threats include herbivory by ungulates and habitat invasion by exotic weeds. Interestingly, the population at Gerry Gulch occurs at a location where the vegetation is significantly impacted by cattle. Herbivory by white-tailed deer has been shown to be a significant factor for population survival in *Polemonium vanbruntiae* Britton (Bermingham 2010). If herbivory by cattle and wildlife affects the survival of *P. elusum*, then the maintenance of ungulate populations below certain levels may be required.

Other aspects of the biology of this taxon are unknown. However, *Polemonium vanbruntiae* is self compat-

ible (Hill et al. 2008). Because reproductive and life history traits influence the survivorship of plant populations, further research on *P. elusum* is necessary in order to develop a more effective conservation strategy.

Molecular analysis.—Sequence data from 28 taxa were analyzed. The 46 vouchers used in this phylogenetic study are listed in Appendix 1. Twenty-six of these were accessions from GenBank. *Leptosiphon*, *Linanthus*, and *Phlox* were used as outgroups because they have been proposed as genera closely related to *Polemonium* (Porter 1997; Johnson et al. 2008; Hankamp 2011).

Field collections of fresh plant material were preserved in silica gel and voucher specimens are deposited in the herbarium at San Francisco State University (Table 1). DNA extracted from herbarium sheets follow the same process. Extraction protocols are described in DNeasy (2004). The ITS1, 5.8S, and ITS2 regions were amplified using primers ITS4 and ITSLEU (White et al. 1990). Both regions were duplicated using standard Polymerase Chain Reaction (PCR) in 25 μ l volume reactions. Excess nucleotides and primers remaining in the samples from the PCR were removed using ExoSAP-it kit.

An Applied Biosystems 3100 Genetic Analyzer was used for the capillary electrophoresis of all samples. Fragments were sequenced using BigDye following the manufacturer's protocols. Precipitation was with EDTA/Ethanol/Sodium acetate, and the remaining cycle sequence products were resuspended in Hi-Di before being denatured. Fragments were visualized using an Applied Biosystems PRISM 3100 Genetic Analyzer. Run modules were conducted using liquid polymer POP-6 or POP-7. Sequence files were base-called using Sequencing Analysis 5.1 (Applied Biosystems 2003), and the forward and reverse reads were formed into a consensus sequence using Sequencher 4.8 (Gene Codes Corporation 2007). The consensus sequence contig was loaded into MacClade 4.08X (Maddison & Maddison 2005) to visually confirm the coherence of the bases, and into ClustalX Version 2 (Larkin et al. 2007) for a complete alignment. The nexus file was analyzed in PAUP 4.0a112 (Swofford 2002), Mr. Bayes 3.1.2 (Ronquist & Huelsenbeck 2003), and GARLI 0.951-GUI (Zwickl 2006).

RESULTS

This ITS data set included 46 samples with a total of 706 characters, 163 of these were variable. Of the variable characters, 61 were parsimony informative. Bootstrap analyses were performed in PAUP 4.0a112 (Swofford 2002) using a heuristic search with 100 repetitions and number of trees increasing by 100. Trees were also analyzed using maximum likelihood and Bayesian analysis.

For statistical selection of the best fit model, jModelTest (Posada 2008) was used. The $-\ln L$ using jModelTest was 2412.83. The results indicated GTR+I+G, and these parameters were employed. Bootstrapping was tested with GARLI and Bayesian analysis provided numbers for branch support.

DISCUSSION

Molecular analysis of the ITS region of *Polemonium* weakly suggests *P. elusum* is sister to *P. mexicanum*, *P. pauciflorum*, *P. grandiflorum*, and *P. carneum* (Fig. 3). This is the best inference from the maximum likelihood tree but it is not statistically supported by either bootstrap (56%) or Bayesian (0.84) values. A few conclusions can be drawn from these results. First, the four species that are most closely related to *P. elusum* are all included in Grant's (1959) sect. *Polemonium* and *P. elusum* also fits into this section. Worley et al. (2009) further divided Grant's sect. *Polemonium* into three species complexes, and except for *P. mexicanum*, the other three species are all included in the *P. pauciflorum* complex. This species complex includes plants that are erect to decumbent. The inflorescences are panicle-like cymes or the flowers are arranged in groups of one to three. *Polemonium elusum* meets these criteria.

Second, under Wherry's (1942) classification, *P. pauciflorum*, *P. grandiflorum*, and *P. carneum* all fall under the large flowered section *Eupolemonium*. Once more, *P. elusum* fits the criteria to be included in this section. These species all have overlapping elevation ranges and low montane habitats but occupy different regions of North America. Although there is not much statistical support for this grouping, morphometric features help validate the placement of *Polemonium elusum* with this group.

Polemonium elusum is congruent with the rest of the genus in its campanulate corolla, habit, compound leaves, stamen attachment, pubescent filaments, and brown seeds. This species notably differs in the calyx

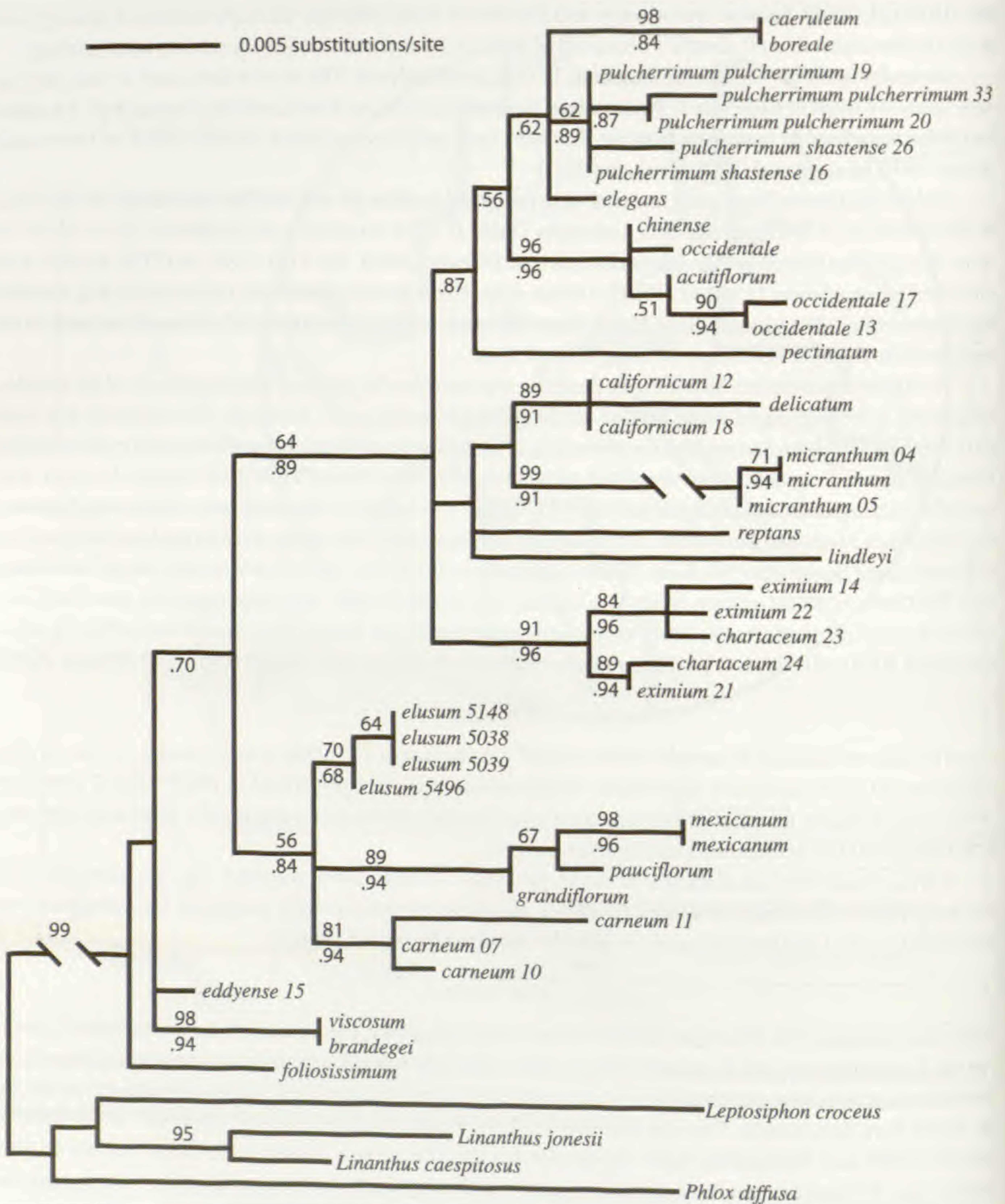


FIG. 3. Maximum likelihood tree for nrITS dataset with GARLI bootstrap values (above branch) and Bayesian posterior probabilities (below branch). $-\ln L = 2412.83$.

membrane and leaf structure. In the calyx, a translucent membrane connects the lobes in *P. elusum* (Fig. 1. A.). A translucent membrane between calyx lobes is exhibited in all of the temperate Polemoniaceae except for *Polemonium*, therefore this is the only species in the genus that is consistent in this attribute with the other genera in the family. This distinction of the calyx tube being translucent between lobes is visible in bud, at anthesis, and also in fruiting. Furthermore, unlike most of the other genera with translucent membranes, in this species the membrane does not rupture in fruit.

Another distinctive feature of *Polemonium elusum* is the leaf structure. The leaf structure and size of *P. elusum* falls on a spectrum between the low and high elevation *Polemoniums*. Though *P. elusum* is not an alpine species, the leaf structure is similar to high elevation *Polemoniums* such as *P. eximium* and *P. viscosum*. As seen in the alpine species, the leaflets in *P. elusum* are deeply lobed, but unlike high elevation *Polemoniums* that have leaflets that are 3–5-lobed, in *P. elusum* the leaves are mostly 2-lobed. Additionally, the compound leaves of alpine species are less than 9 mm wide while in *P. elusum* the leaves grow up to 30 mm wide. Similarly larger leaves are seen in lower elevation *Polemoniums*, like those of *P. caeruleum* and *P. carneum*, but the leaflets in these species are entire and not lobed.

APPENDIX 1

Voucher specimen for the 46 populations of 29 taxa from which nrITS region sequences were obtained. All samples without GenBank accession numbers were placed in silica gel in the field by Stubbs. Material of *P. elusum* was from dried specimens collected by Irwin.

Taxon	Voucher/GenBank #
<i>P. acutiflorum</i>	de Nevers 2073 / DQ320767
<i>P. boreale</i>	Cody 26927 / DQ320769
<i>P. brandegei</i>	Worley 006 / DQ320771
<i>P. caeruleum</i>	McNeal 3530, BRY / EU628253
<i>P. californicum</i>	Stubbs 18, SFSU
<i>P. californicum</i>	Stubbs 18, SFSU
<i>P. carneum</i>	Stubbs 07, SFSU
<i>P. carneum</i>	Stubbs 10, SFSU
<i>P. carneum</i>	Stubbs 11, SFSU
<i>P. chartaceum</i>	Stubbs 24, SFSU
<i>P. chartaceum</i>	Stubbs 23, SFSU
<i>P. chinense</i>	Ting-nong 1543 / DQ32078
<i>P. eddyense</i> comb. nov.	Stubbs 15, SFSU
<i>P. elegans</i>	Worley 18 / DQ320783
<i>P. elusum</i>	Irwin 5038, RM
<i>P. elusum</i>	Irwin 5039, RM
<i>P. elusum</i>	Irwin 5148, RM
<i>P. elusum</i>	Irwin 5496, RM
<i>P. eximium</i>	Stubbs 14, SFSU
<i>P. eximium</i>	Stubbs 21, SFSU
<i>P. eximium</i>	Stubbs 22, SFSU
<i>P. foliosissimum</i>	Halse 4261 / DQ320787
<i>P. grandiflorum</i>	Zamudio 7469 / DQ320788
<i>P. mexicanum</i>	Koch 75399 / DQ320789
<i>P. micranthum</i>	Stubbs 04, SFSU
<i>P. micranthum</i>	Stubbs 05, SFSU
<i>P. micranthum</i>	Taylor 12548 / DQ320791
<i>P. occidentale</i>	Stubbs 17, SFSU
<i>P. occidentale</i>	Timme 015 / DQ320793
<i>P. occidentale</i>	Stubbs 13, SFSU
<i>P. pauciflorum</i>	LeBuhn s.n. / DQ320794
<i>P. pectinatum</i>	Worley 001 / DQ320796
<i>P. pulcherrimum</i> var. <i>delicatum</i>	de Geofroy 127 / DQ320797
<i>P. pulcherrimum</i> var. <i>lindleyi</i>	Grimes 2159 / DQ320801
<i>P. pulcherrimum</i> var. <i>pulcherrimum</i>	Stubbs 19, SFSU
<i>P. pulcherrimum</i> var. <i>pulcherrimum</i>	Stubbs 33, SFSU
<i>P. pulcherrimum</i> var. <i>pulcherrimum</i>	Stubbs 20, SFSU
<i>P. pulcherrimum</i> var. <i>shastense</i>	Stubbs 16, SFSU
<i>P. pulcherrimum</i> var. <i>shastense</i>	Stubbs 26, SFSU
<i>P. reptans</i>	Keil 6266 / DQ320805
<i>P. viscosum</i>	Worley 004 / DQ320806
<i>Leptosiphon croceus</i>	Hankamp 043, SFSU
<i>Linanthus caespitosus</i>	Wilken 13982, SFSU/AF119443
<i>Linanthus jonesii</i>	Owings 047, SFSU/AF119430
<i>Phlox diffusa</i>	Peterson 97-110, SFSU/AF119444

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REFERENCES

- APPLIED BIOSYSTEMS. 2003. Sequencing Analysis® version 5.1. <http://www.appliedbiosystems.com>.
- BERMINGHAM, L.H. 2010. Deer herbivory and habitat type influence long-term population dynamics of a rare wetland plant. *Pl. Ecol.* 210:359–378.
- DNEASY, Q. 2004. Plant DNA extraction handbook. <http://www.qiagen.com>.
- GENE CODES CORPORATION. 2007. Sequencher® version 4.8 sequence analysis software. Ann Arbor, MI. <http://www.gene-codes.com>.
- GRANT, V. 1959. Natural history of the Phlox family, vol. 1, systematic botany. The Hague: Martinus Nijhoff.
- HANKAMP, P.Z. 2011. Molecular systematics of *Leptosiphon* (Polemoniaceae). M.S. thesis. San Francisco State University, CA.
- HARTMAN, R.L. 1992. The Rocky Mountain Herbarium, associated floristics inventory, and the Flora of the Rocky Mountains project. *J. Idaho Acad. Sci.* 28:22–43.
- HARTMAN, R.L. AND B.E. NELSON. 2011. General information for floristics proposals. [The Boiler Plate]. <http://www.rmh.uwyo.edu>.
- HARTMAN, R.H., B.E. NELSON, AND B. LEGLER. 2009. Rocky Mountain Herbarium Specimen Database. <http://www.rmh.uwyo.edu>
- HILL, L.M., A.K. BRODY, AND C.L. TEDESCO. 2008. Mating strategies and pollen limitation in a globally threatened perennial *Polemonium vanbruntiae*. *Acta Oecol.* 33:314–323
- JOHNSON, L.A., L.M. CHAN, T.L. WEESE, L.D. BUSBY, AND S. McMURRY. 2008. Nuclear and cpDNA sequences combined provide strong inference of higher phylogenetic relationships in the phlox family (Polemoniaceae). *Molec. Phylogen. Evol.* 48:997–1012.
- KESONIE, D. (SCOTT) AND R.L. HARTMAN. 2011. A floristic inventory of Grand Teton National Park, Pinyon Peak Highlands, and vicinity, Wyoming, U.S.A. *J. Bot. Res. Inst. Texas* 5:357–388.
- KUHN, B, B.E. NELSON, AND R.L. HARTMAN. 2011. A floristic inventory of the Cimarron National Grassland (Kansas) and the Comanche National Grassland (Colorado). *J. Bot. Res. Inst. Texas* 5:753–772.
- LARKIN, M.A., G. BLACKSHIELDS, N.P. BROWN, R. CHENNA, P.A. McGETTIGAN, H. McWILLIAM, F. VALENTIN, I.M. WALLACE, A. WILM, R. LOPEZ, J.D. THOMPSON, T.J. GIBSON, AND D.G. HIGGINS. 2007. Clustal W and Clustal X version 2.0. *Bioinformatics* 23:2947–2948.
- MADDISON, D.R. AND W.P. MADDISON. 2005. MacClade 4: Analysis of phylogeny and character evolution. Version 4.08 for OSX. Sinauer Associates, Sunderland, MA.
- PORTER, J.M. 1997. Phylogeny of the Polemoniaceae based on nuclear internal transcribed spacer DNA sequences. *Aliso* 15:57–77.
- POSADA, D. 2008. jModelTest: phylogenetic model averaging. *Molec. Biol. Evol.* 25:1253–1256.
- REIF, B, J. LARSON, B. JACOBS, B.E. NELSON, AND R.L. HARTMAN. 2009. Floristic studies in north central New Mexico, U.S.A. The Tusas Mountains and the Jemez Mountains. *J. Bot. Res. Inst. Texas* 3:921–961.
- RONQUIST, F. AND J.P. HUELSENBECK. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574.
- SWOFFORD, D.L. 2002. PAUP*. Phylogenetic analysis using parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, MA.
- WHITE, T.J., T.D. BRUNS, S.B. LEE, AND J.W. TAYLOR. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis, M.A., D.H. Gelfand, J.J. Sininsky, and T.J. White, eds. PCR protocols: a guide to methods and applications. Academic Press Inc., San Diego, CA. Pp. 315–322.
- WHERRY, E.T. 1942. The genus *Polemonium* in America. *Amer. Midl. Naturalist* 27:741–760.
- WORLEY, A.C., H. GHAZVINI, AND D.W. SCHEMSKE. 2009. A phylogeny of the genus *Polemonium* based on amplified fragment length polymorphism (AFLP) markers. *Syst. Bot.* 34:149–161.
- ZIENTEK, M.L., P.D. DERKEY, AND R.J. MILLER 2005. A spatial database for the geology of Northern Rocky Mountains. U.S. Geological Survey, Menlo Park, CA. <http://pubs.usgs.gov/of/2005/1235>.
- ZWICKL, D.J. 2006. Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. Ph.D. dissertation, The University of Texas at Austin.